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JOHN G. MAISEY[1]

ABSTRACT

Evidence and opinions on the nature and diversity of elasmobranch jaw suspension are discussed and the phylogenetic implications of some of these differences are considered. The hyomandibula is attached to the mandibular joint in all living elasmobranchs, and all are therefore hyostylic with respect to the hyomandibula. Amphistyly is a subset or condition of hyostyly rather than an alternative mode of jaw support. Living osteichthyans and perhaps acanthodians are similarly hyostylic, and there is no reason to suppose that this condition is anything but a primitive gnathostome character. Some elasmobranchs have an orbital process which has a consistent relationship to nerves and vessels within the orbit. It is possible to use this relationship systematically to define a group of "orbitostylic" sharks in a novel way. The orbital process does not seem to correspond to the "basal articulation" of acanthodians and osteichthyans.

INTRODUCTION

Sharks and rays (collectively termed elasmobranchs) and chimaeroids or rabbit fishes are customarily classified together as chondrichthyans. Although it is fairly safe to regard chimaeroids and Recent elasmobranchs as sister groups, there is much uncertainty surrounding the relationships of fossil and recent chondrichthyans. However, for the purposes of this paper, elasmobranchs are regarded as all sharklike chondrichthyans, since elasmobranchs and chimaeroids have profoundly different jaw apparatus. The mandibular peculiarities of chimaeroids are not discussed; the main purpose of the present paper is to consider variation in elasmobranch jaw suspension, which has long been of interest to ichthyologists. For years, students have been informed that amphistylic jaws are more primitive than hyostylic ones, and the concepts of hyostylic, amphistylic, and holostylic suspension are now entrenched, even though authors disagree about their definitions. Improved knowledge of living and fossil sharks reveals inadequacies in these concepts, however. I will review chondrichthyan jaw suspensions from both phylogenetic and functional viewpoints based in part on new information.

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ABBREVIATIONS

ANATOMICAL

b. art, basal articulation
e. art, ethmoidal articulation
eps, foramen for efferent pseudobranchial artery
hm, hyomandibula
op, orbital process of palatoquadrate
p. art, postorbital articulation
pq, palatoquadrate
r, rostrum
II, optic foramen

INSTITUTIONAL

AMNH, American Museum of Natural History
BM(NH), British Museum (Natural History)
MCZ, Museum of Comparative Zoology, Harvard University
NMNH, National Museum of Natural History, Smithsonian Institution

JAW ARRANGEMENTS IN PRIMITIVE GNATHOSTOMES

The jaws and visceral arches have, since Gegenbaur (1872), long been regarded serially homologous structures, sharing a fundamental segmented pattern, but exhaustive studies since then have failed to provide evidence for the earlier existence of supposedly "missing" components of the mandibular and hyoid arch. Only the epi-elements and cerato-elements appear to be serially homologous in the jaws and visceral arches, and even here there is doubt as to whether some of the elements (particularly the palatoquadrate and hyomandibula) are homologous in every respect in different groups of gnathostomes (Jollie, 1971b). Nelson (1969) suggested that serial homology of all components is unnecessary and extreme, and that non-homologous elements of the prootic arches might have existed. Jollie (1971b) took this idea further and proposed that the "missing" dorsal elements (pharyngomandibular and pharyngohyal) never existed as such, and that their blastemic tissues instead became incorporated into the primitive gnathostome braincase (as trabeculae and lateral commissures, respectively). At a later stage in this scenario, mesenchymal tissue dorsal and ventral to the epi-elements and cerato-elements differentiated into the familiar pharyngo-elements, hypo-elements, and basi-elements. Differences between these elements in osteichthyans and chondrichthyans might indicate their independent acquisition in these groups (Jollie, 1971b, p. 93).

Such a hypothesis can be neither confirmed nor refuted while "missing" elements remain unidentified in supposedly serially homologous visceral arches. But it comes closer to observed embryological and paleontological data than other proposals, such as the scenario that the hyoid and mandibular arches were originally separate in "aphetohyoidean" acanthodians (Watson, 1937) or symmoriid elasmobranchs (Zangerl and Williams, 1975; Zangerl and Case, 1976). That either group was aphetohyoidean is questionable both on embryological and on paleontological grounds. In living osteichthyans and chondrichthyans the hyoid arch is attached to the mandible close to the jaw joint, and instead of a complete hyoidean gill opening there is a small spiracle which can, in many osteichthyans and some carcharhinid sharks, become completely closed. It is more parsimonious to argue that mandibular-hyoid attachment occurred only once in gnathostome history, than to propose convergence as an explanation. Miles (1968) showed that *Acanthodes* was functionally amphistylic, and suggested (Moy-Thomas and Miles, 1971) that other acanthodians such as *Climatius* may have lacked a postorbital articulation between the palatoquadrate and neurocranium, and were probably hyostylic. I have examined a three-dimensionally preserved upper Devonian elasmobranch, NMNH 20675, in which the jaws, visceral skeleton, and muscle impressions are preserved. It clearly had five lateral gill openings and no hyoidean gill cleft, but in all probability had a spiracle (Maisey, in preparation). Interestingly, it has a similar pectoral fin skeleton to supposedly "aphetohyoidean" symmoriids.

The significance of DeBeer and Moy-Thomas's (1935) interpretation of the hyoid arch in chimaeroids remains uncertain in the continued absence of detailed embryological studies at earlier stages than they examined.

At present the data is ambiguous, since trabeculae are present (presumably produced from presumptive pharyngomandibular blastemas) and there is cartilage (in part a lateral commissure?) lateral to the head vein, but otherwise there is little to suggest incorporation of pharyngoblastemic tissue into the braincase (DeBeer and Moy-Thomas, 1935; Jollie, 1971a).

DeBeer (1937) and Schaeffer (1975) advocate that a pharyngohyal was primitively present in gnathostomes and was independently lost in the placoderms, chondrichthyans (retained in chimaeroids), and osteichthyans mainly because of different relationships between the lateral head vein, hyomandibular nerve and proximal part of the hyomandibula. Jollie (1971a, p. 37) notes that pharyngohyal incorporation into the braincase seems very different in teleostomes and chondrichthyans, but argues that these differences could be accounted for just as easily by evolutionary changes as by independent acquisition; one could argue that the differences in hyomandibular attachment can be similarly explained.

The consistency in position of the hyomandibula in all living elasmobranchs, both in relation to the glossopharyngeal nerve and to the jugular canal, is probably a primitive elasmobranch synapomorphy since the same condition prevails in *Hybodus basanus*, other hybodontids (Maisey, in preparation), and in Permian xenacanths (Schaeffer, personal commun.). A separate pharyngohyal has not been unequivocally demonstrated in any elasmobranch, and available data suggest that it was never present as such. Miles (1968) believes that the hyomandibula of acanthodians played a part in jaw support, as in osteichthyans and chondrichthyans. Jollie's (1971a and 1971b) interpretation of embryological data, and the evidence available from fossils all suggest that hyoid support (i.e., hyostyly in a broad sense) is primitive to all major gnathostome groups, and that hyostyly may be regarded as a gnathostome synapomorphy.

Jarvik (1977) regards the contact anteriorly of the right and left palatoquadrate, to form a symphysis or commissure, as a characteristic of sharks (i.e., an elasmobranch synapomorphy). The palatoquadrates of *Hybodus* and many Paleozoic sharks do not meet, however, and may be separated by the rostrum. Anteriorly separated palatoquadrates therefore appear to be the primitive elasmobranch condition. This is also the condition in acanthodians and osteichthyans (Moy-Thomas and Miles, 1971) and it is therefore probably a basic gnathostome feature. In some living sharks, such as hexanchoids, the palatoquadrate symphysis is very weak, and it is only well developed in relatively derived squaloids and galeomorphs.

An ethmoidal articulation may be primitively present in all gnathostomes, but is unknown in acanthodians. Jollie (1971a, 1971b) notes that the developing palatoquadrate maintains a connection with the anterior ends of the trabecula and regards this as a primitive gnathostome condition.

The palatoquadrate of Recent sharks is attached to the neurocranium both preorbitally and postorbitally, although the degree of attachment and consequent mobility of the jaws is highly variable. In batoids the palatoquadrate is supported by ligaments and by the hyomandibula, but makes no immediate contact with the neurocranium. In sharks there may be a well-developed ethmoidal articulation, sometimes (e.g., *Heterodontus*) with a pronounced ethmoidal groove into which the palatoquadrate fits anteriorly. In many forms this articulation is loose and ligamentous (see below).

The palatoquadrates of many Paleozoic elasmobranchs (cladoselachians, symmoriids, ctenacanths, xenacanths) have an expanded otic flange postorbitally, the anterodorsal margin of which articulates with the posterior surface of the postorbital process. A similar otic flange is restricted among living sharks to hexanchoids. Outgroup comparison with acanthodians and osteichthyans suggests that the expanded flange may be another primitive gnathostome feature which has become lost (or modified) in many elasmobranchs (see p. 5) and perhaps in some acanthodians (Moy-Thomas and Miles, 1971, p. 69). A double mandibular joint is present in living and fossil elasmobranchs and *Acan-*

thodes, and may represent a synapomorphy (Jarvik, 1977), but is absent in chimaeroids (perhaps as response to holostyly) and osteichthyans.

A direct postorbital articulation is either present (hexanchoids) or absent (most other living sharks), except that in some forms the palatoquadrate may meet the postorbital process at some point in mandibular kinesis (Compagno, 1977); this postorbital contact need not therefore be wholly suspensory.

Even where no postorbital contact is made, however, a ligament joins the dorsal margin of the quadrate region to the postorbital process of the braincase. Additionally, the hyomandibula is attached to the mandibular arch, lending support to the jaws, especially in elasmobranchs where the postorbital articulation is reduced. The dorsal end of the hyomandibula invariably articulates with the lateral wall of the otic capsule, immediately anterior to the exit for the glossopharyngeal nerve (Schaeffer, personal commun.).

TRADITIONAL VIEWS OF ELASMOBRANCH JAW SUSPENSION

A useful review of attempts to categorize jaw suspensions of elasmobranchs appears in Smith (1942, p. 699). The original concepts of hyostyly, amphistyly and holostyly stem from Huxley (1876) but were modified by Goodrich (1909) and it is essentially his views on the subject which are reiterated in most anatomical textbooks.

In Huxley's (1876) amphistylic condition, the palatoquadrate is entirely suspended from the braincase by ligaments. The hyomandibula is less important in supporting the jaws, even though it is ligamentously joined to them. A postorbital articulation was not mentioned, this requirement being added by Goodrich (1909, p. 95) in an attempt to remedy what were seen as shortcomings in the original concept. A major problem of Huxley's (1876) definition is that all elasmobranch palatoquadrates are suspended by ligaments from the braincase, including sharks customarily regarded as "hyostylic." Furthermore, the elasmobranch epihyal element is always a functional hyomandibula since it is attached distally to the jaws. Goodrich (1909) effectively circumvented the first problem by including an additional requirement for amphistyly (the postorbital articulation), but was unable to get around the second problem (the hyostylic hyomandibula). Therefore, neither his nor Huxley's (1876) "hyostylic" suspension is clearly separable from the original definition of amphistyly, in which the palatoquadrate is suspended by ligaments and a hyomandibula.

Nevertheless, there are important differences between the relatively mobile jaws of many recent elasmobranchs and the more firmly articulated jaws of other forms, including the majority of fossil sharks. The forms which would traditionally be called "hyostylic" are provided with considerable mandibular kinesis which facilitates jaw protraction (Luther, 1908; Haller, 1926; Zlabek, 1931; Moss, 1962, 1972). The hyomandibula plays an important part in supporting the jaws (Huxley, 1876), and is usually much larger than the epibranchials. When the jaws are retracted, an inelastic ethmoidal ligament is folded between the dorsal surface of the palatine region and preorbital part of the braincase. At full protraction this ligament is taut (Moss, 1962, 1972). It is best developed in lamnoids and carcharhinoids, but there is disagreement over the degree of separation between the palatoquadrate and braincase. Smith (1942, p. 699) noted, "In the hyostylic skull the upper jaw is held somewhat away from the cranium, and retains a considerable degree of mobility." He uses *Scyliorhinus (Scyllium)* as an example, after Goodrich (1909, fig. 59c), but Garman (1913) showed that in *Lamna* the "orbital process" (actually a low palatine process anterior to the position of a true orbital process—see below), is close to, or in contact with, the ethmoidal region. This seems to be true of other galeomorphs also (Compagno, 1977). Thus, even in sharks with highly kinetic jaws the palatoquadrate may be braced against the neurocranium preorbitally, at some point in jaw movement. Contact would normally be made when the jaws are retracted; at full pro-

traction they would be positioned as Goodrich (1909) and Smith (1942) indicate (see Moss, 1962, 1972 for details).

Although some sharks have highly kinetic jaws, they cannot be contrasted sharply with other sharks having less mobile apparatus. It is here that the shortcomings of Huxley's (1876) and Goodrich's (1909) concepts of hyostyly and amphistyly become most apparent. For example, *Chlamydoselachus* was not amphistylic according to Goodrich (1909), since the palatoquadrate lacks a postorbital articulation (Allis, 1923; Smith, 1942), but Compagno (1977) reports that in some specimens, postorbital contact occurs when the jaws reach a certain position (limited protraction being possible). In *Heterodontus* the palatoquadrate fits into a pronounced ethmoidal groove anteriorly and never disarticulates even at maximum protraction. The jaws are therefore strongly buttressed anteriorly in addition to receiving hyomandibular support posteriorly. Smith (1942) also noted the presence of fibrous tissues in the orbital region, and commented that *Heterodontus* hardly conforms to the hyostylic pattern it is supposed to represent.

It seems that if we are to salvage anything useful from Huxley's (1876) and Goodrich's (1909) work on jaw suspension, we must discard their concepts of hyostyly and amphistyly as separate, alternative entities. Instead, we should look for common characteristics and see whether different patterns of jaw support can be distinguished within this framework. One important consistency among elasmobranchs is the hyomandibular support of the jaws already mentioned. Even in "amphistylic" sharks the hyomandibula is suspensory (i.e., hyostylic). Amphistyly is therefore a (probably primitive) state of hyostyly. The hyomandibula is similarly hyostylic in teleostomes, although as is well known there are differences in its relationship to the lateral head vein and other structures between teleostomes and elasmobranchs (DeBeer, 1937; Schaeffer, 1975), and in osteichthyans additional support is given to the palatoquadrate by dermal bones. Other differences between teleostomes and elasmobranchs are to be found in the sites of palatoquadrate articulations with the braincase (Miles, 1968). Among elasmobranchs most of the variation in jaw suspension is accounted for by differences in the sites and relative development of palatoquadrate-braincase attachments.

POTENTIAL ARTICULATIONS BETWEEN PALATOQUADRATE AND NEUROCRANIUM

Throughout its length the gnathostome palatoquadrate is connected to the neurocranium by connective tissue. Within this, several articulations or ligamentous attachments may develop (fig. 1). There is an ethmoidal articulation (apparently absent in acanthodians; Miles, 1968) which may be accompanied by a rostral articulation. Both articulations are developed in some fossil elasmobranchs, e.g., *Hybodus* and *Xenacanthus*. Within the orbit there may be an orbital articulation (in some living elasmobranchs) or a slightly more posterior basal articulation (acanthodians, osteichthyans, see Holmgren, 1942; Miles, 1968; Jollie, 1971a). There may be a postorbital articulation, and behind this an indirect articulation with the neurocranium via the hyomandibula. No gnathostome is known with all these attachments and articulations, and figure 1 is not therefore regarded as representing a gnathostome morphotype. Some attachments, or combinations thereof, may, however, be derived characters for major gnathostome groups.

ELASMOBRANCH PALATOQUADRATE ATTACHMENTS AND THE ACANTHODIAN "ORBITAL PROCESS"

In some living and many fossil elasmobranchs (lamnoids, carcharhinoids, hybodontids, cladoselachians, ctenacanths, xenacanths, symmoriids) there is a pronounced ethmoidal articulation with the basicranium in the extreme anterior part of the orbit. In *Hybodus* and xenacanths the palatine part of the palatoquadrate extends anteriorly to either side of the rostrum which effectively prohibits a palatoquadrate commissure or symphysis from developing. In *Chlamydoselachus* the jaws are similarly elongated,

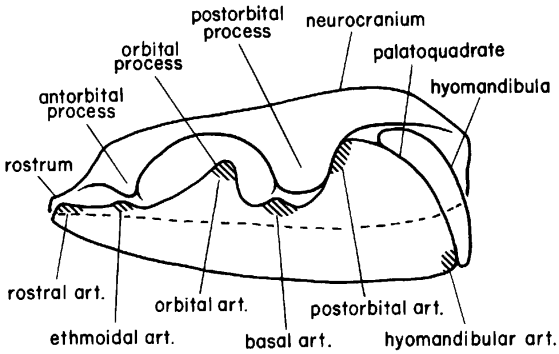

FIG. 1. Areas of attachment between palatoquadrate and braincase in a hypothetical gnathostome. No living or fossil form has all these attachments.

but the palatoquadrates meet at a feeble symphysis and a rostrum is not developed. There is no palatine process on the palatoquadrate. The dorsolateral surface of its palatine ramus makes a sliding contact with the inner surface of the ectethmoid process, beneath and slightly behind the olfactory capsules. This ethmoidal articulation is well developed in carcharhinoids, which often have a thickening of the ectethmoid cartilage anteromedial to the palatine process of the palatoquadrate. There is a massive ethmopalatine ligament passing between the two "articular" surfaces. The palatine process is mainly an anchor for the ethmopalatine ligament, and only its anterolateral surfaces come close to the ectethmoid articulation.

An orbital process arises behind the ethmoidal articulation in some living elasmobranchs (*Chlamydoselachus, Squatina, Pristiophorus,* hexanchoids, and squaloids). Embryologically it is the anterior of two potential articulations within the orbit (Holmgren, 1942; Miles, 1968) and invariably lies behind the optic foramen and anterior to the efferent pseudobranchial foramen, optic pedicel, and rectus muscle complex. The more posterior articulation fails to develop in elasmobranchs (Holmgren, 1942) but according to Miles (1968) forms the basal articulation of acanthodians and osteichthyans. In osteichthyans the efferent pseudobranchial foramen is located anterior to the palatobasal (basipterygoid) process and its attachment to the palatoquadrate. A palatobasal process has been identified in squaloids and hexanchoids, at the site of the polar cartilage (DeBeer, 1937; Jollie, 1962, 1971a). While this at first seems to correspond to the basipterygoid process as defined by DeBeer (1937), there is no evidence that it forms a palatobasal articulation with the palatoquadrate even through this articulation can be very close to the process in squaloids and hexanchoids (Holmgren, 1942, 1943; Miles, 1968, p. 238; Jollie, 1971a, p. 32).

In *Chlamydoselachus* and *Squatina* the orbital articulation is farther forward on the orbital wall than in squaloids and hexanchoids, and is not associated with a basipterygoid process nor with that part of the braincase derived from the polar cartilages. Thus, among neoselachians with an orbital articulation, only some approach the osteichthyan condition with a basipterygoid process, and there is good evidence, from an outgroup comparison with other living and fossil sharks, that this similarity with osteichthyans has arisen secondarily.

If Miles (1968) has correctly interpreted the acanthodian basal articulation along osteichthyan lines, Jarvik's (1977) argument for homology between the elasmobranch orbital process and acanthodian basal process is spurious. In addition to Holmgren's (1942) and Jollie's (1971a) embryological data, which seem to support Miles (1968), I would add that no acanthodian or osteichthyan has an orbital process positioned as in elasmobranchs anterior to the efferent pseudobranchial foramen (cf. figs. 2, 3). Jarvik's own illustrations (e.g., 1977, figs. 3, 8) indicate that in *Acanthodes* this foramen opens anterior to the basal process, as in osteichthyans (fig. 2A, B). Jarvik (*ibid.*) also attempts to homologize the ethmoidal articulation of Paleozoic sharks with the orbital (palatobasal) articulation of Recent forms despite their different topographic relationships to structures within the orbit. The well-developed anterior palatoquadrate articulation of living galeomorphs seems to correspond with the ethmoidal articulation of *Xenacanthus* and *Hybodus* rather than the orbital articulation,

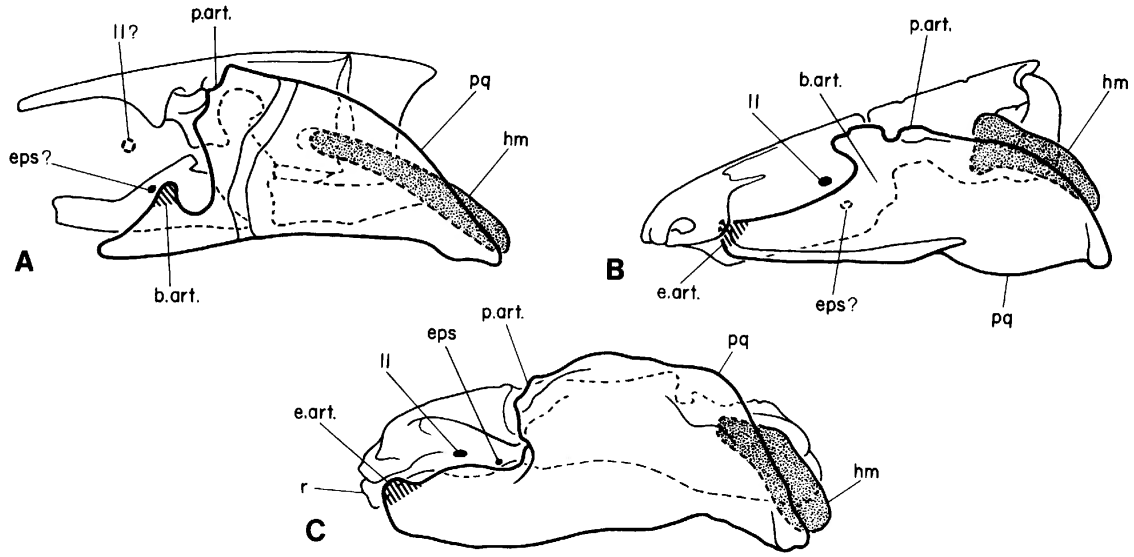

FIG. 2. Palatoquadrate and hyomandibular articulations in various gnathostomes. A, *Acanthodes*, a late acanthodian; B, *Eusthenopteron* a rhipidistian osteichthyan; C, *Xenacanthus*, an elasmobranch. (A, after Miles, 1968 and Jarvik, 1977; B, after Jarvik, 1937; C, original).

since it is invariably far forward on the basicranium. Moreover, in *Squalus* there is a weak ethmoidal articulation anterior to the orbital one (Jollie, 1962, fig. 5.16B). In view of their distinctiveness, it seems best to regard the orbital and ethmoidal attachments as being different.

The postorbital articulation is restricted today to hexanchoid sharks (fig. 3C). Elsewhere (Maisey, in preparation), I have identified several synapomorphies for living elasmobranchs, including hexanchoids, suggesting that they form a monophyletic group whose sister group is the hybodontid sharks. *Hybodus basanus* has no postorbital articulation with the neurocranium (see below), but there is a strong ethmoidal articulation and a well-developed hyomandibula. The arrangement is similar to that of *Heterodontus*, but there are differences in the arrangement of the hyomandibula, which in *Hybodus* passes dorsal to the palatoquadrate (fig. 6D, E).

If hybodontids are the sister group to all neoselachians, either the postorbital articulation of the palatoquadrate has been lost independently in both groups but retained by hexanchoids, or it was lost at an earlier stage and then reacquired by hexanchoids. The second alternative has never been seriously explored, and evidence for it is slight. If neoselachians and hybodontids primitively had the postorbital articulation, we might expect to find some evidence of it in primitive hybodontids, just as we do in hexanchoids, since it would be primitively present in the sister group to all these forms. The jaws of a Triassic hybodontid shark seem to have a weak postorbital articulation (Thomson, personal commun.). Confirmation of such a palatoquadrate articulation supports an interpretation that the postorbital articulations in neoselachians and hybodontids have been lost independently.

PHYLOGENETIC COMMENTS ON THE ORBITAL PROCESS OF NEOSELACHIANS

In *Chlamydoselachus* the orbital process articulates with the braincase close to the antorbital wall, rising dorsally into the orbit

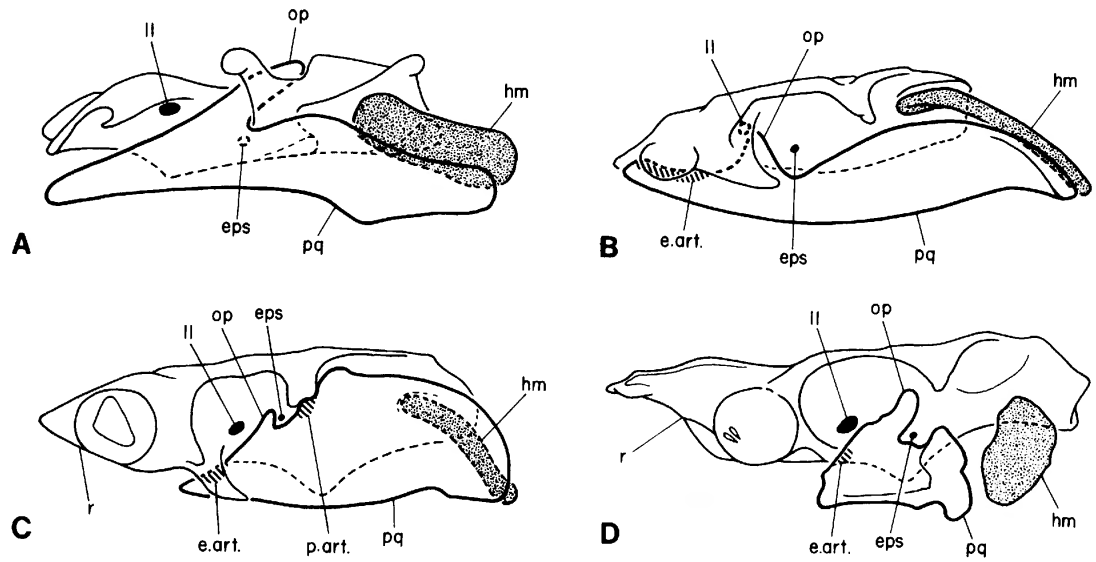

FIG. 3. Palatoquadrate and hyomandibular articulations in various orbitostylic elasmobranchs. A, *Squatina*; B, *Chlamydoselachus*; C, *Heptranchias*; D, *Squalus*. Note consistency of relationship between orbital process of the palatoquadrate and structures identified within the orbit. In *Squatina* the efferent pseudobranchial foramen seems mesial to the orbital process but is behind the process when the jaw is protracted. (All originals.)

immediately behind the optic foramen and anterior to the optic pedicel, rectus musculature and efferent pseudobranchial artery (fig. 3B). Other sharks with a corresponding orbital process in this position include the hexanchoids, squaloids, *Squatina* and *Pristiophorus*. No other elasmobranchs, living or fossil, have a comparable process, and I regard this as a shared derived character defining a monophyletic group of neoselachians. There are no conflicting characters to suggest that this derived condition has evolved more than once.

In *Squatina* the orbital process is greatly enlarged, passes diagonally through the orbit and projects distally above the supraorbital shelf. In hexanchoids and squaloids the process articulates with the braincase near to the postorbital process, immediately anterior to the basipterygoid (palatobasal) process. The orbital process therefore displays a high degree of variation in its position within the orbit, yet retains a remarkably consistent relationship to the landmarks mentioned (fig. 3).

The likelihood that the orbital process can be used to define a major monophyletic group led me to consider the possible interrelationships of the forms in question. The comments which follow are not intended to be definitive; there are still many unanswered questions and some of my characters are conflicting, but I offer them to promote discussion and provoke further comments.

The orbital process as defined above, and its corresponding articulation on the neurocranium (characters 4 and 5 of Holmgren, 1941) define node 1 on my cladogram (fig. 4). The group so defined has neven been previously identified in any taxonomic study and is therefore unnamed. I propose referring to them as orbitostylic elasmobranchs to distinguish them from other neoselachians.

The flattened shape of *Squatina* is reminiscent of batoids, but is of uncertain taxonomic value. The orbital process is greatly elongated, and perforates the supraorbital crest, the pectoral fins are expanded anteriorly and separated from the head by a notch (although a similar notch is probably

present in *Belemnobatis annectans*, see Maisey, 1976). The first vertebral centrum is expanded laterally and may fuse with the second to form a synarcual which has been compared to those of batoids (Compagno, 1977). The arrangement in *Squatina* is, however, much closer to that found in orectoloboids and chiloscyllids (Case, personal commun.), and is possibly a shared derived character of those forms which would bear further investigation.

Squatina is placed as a primitive sister group to other orbitostylic elasmobranchs because it lacks certain characters which define node 2 on the cladogram. These characters include the presence of an open ectethmoid chamber (Holmgren, 1941; character 34), loss of nasoral grooves, loss of a subocular shelf (vestigial in *Chlamydoselachus* embryos), and presence of a basal angle (weakly developed in *Chlamydoselachus*), produced where the embryonic trabeculae meet the rest of the basicranium in the hypophyseal region.

The sharks defined by node 2 have been termed squalomorphs by Compagno (1973, 1977), although he does not use all the characters I have listed, and uses the "basal" articulation of the orbital process as a synapomorphy, whereas I regard it as already primitive at this level. He includes as a further synapomorphy the presence of the levator labii superioris 2 of Daniel (1934).

Chlamydoselachus is somewhat borderline in two of my characters (absence of subocular shelf, presence of basal angle) and is probably autapomorphic in several respects, e.g., its curious dentition (previously supposed to indicate "cladodont" or xenacanth affinity; see Gudger and Smith, 1935), length of first branchial arch, and anguilliform shape.

Node 3 on my cladogram is defined by a narrowing of the basicranium anterior to the palatobasal process (Holmgren, 1941; character 2), and a relative shift in the orbital articulation to the back of the orbit. This node would be easier to define were it possible to include the additional characters used to define node 3a, but in two important respects (see 3a below), *Heptranchias* seems

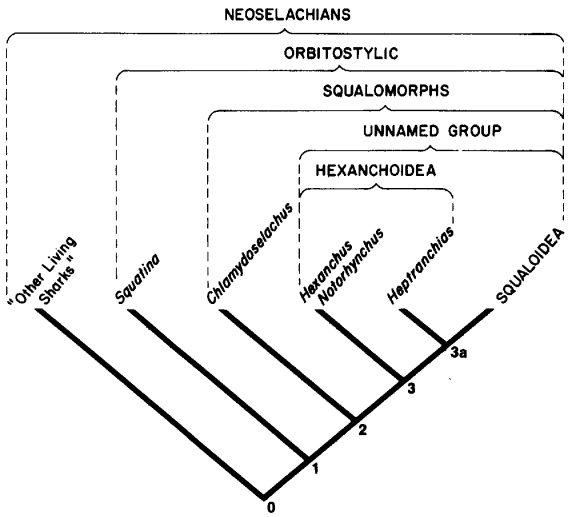

FIG. 4. Cladogram of relationships suggested in the text. According to the characters used, hexanchoids are paraphyletic. Characters defining node 0 are discussed elsewhere; other nodes are characterized in the text.

closer to squaloids than to other hexanchoids (*Hexanchus, Notorhynchus*). Other characters of admittedly questionable significance at node 3 include the tooth crown which is reclined on its basal plate (at least in the lower teeth of hexanchoids and squaloids, and in the uppers of presumably more specialized squaloids), and perhaps also the presence of the adductor γ muscle of Luther (1908).

Node 3a is defined by the presence of a basal communicating canal through the internasal septum, and by the presence of a median keel on the internasal plate. In both respects *Heptranchias* is closer to squaloids than to other hexanchoids (even though the median keel is only present in embryo *Heptranchias* and is weak in some squaloids—see Holmgren, 1941). Compagno (1977) uses both these characters to define squaloids, but so doing requires the inclusion of *Heptranchias* within the group.

There are grounds for retaining the hexanchoids as a monophyletic group. Characters which support this include the lack of propterygial radials, the presence of more than five gill slits and only one dorsal fin, and

the dentition of upper prehensile teeth and lower serrated ones. Other characters listed by Compagno (1977) as hexanchoid synapomorphies are unconvincing, e.g., lack of lateral commissure (widespread among neoselachians), elongate ectethmoid process (present in *Chlamydoselachus,* some squaloids and other neoselachians, and *Hybodus*), and lack of finspines (many neoselachians and fossil elasmobranchs). One of the most striking similarities between hexanchoids is their jaws, with a strong postorbital articulation and otic process, but this may simply be a primitive condition (see above). The high number of gill arches (six or seven) is impressively consistent, but its value as a synapomorphy is lessened by reports of a sixth branchial arch in a wide variety of elasmobranchs, including *Pristiophorus* (Regan, 1906, p. 740), *Heterodontus* and "some of the rays" (Hawkes, 1906; Daniel, 1934; p. 65) and *Galeocerdo* (Hamdy, 1973, p. 83).

Compagno (1977) defines the squaloids on the basis of two characters which also occur in *Heptranchias* (see above), and which are therefore inadmissable at the squaloid level (node 4 here). In fact, I have found it extremely difficult to find squaloid synapomorphies, many of the characters suggested by others for uniting them being either primitive, e.g., presence of finspines, retention of lateral commissure around the jugular canal, or not restricted to squaloids, e.g., lack of anal fin (also squatinoids, pristiophoroids and batoids), reduction or absence of anterior extensions of the lateral aortae over the palate (also *Heterodontus,* orectoloboids, and chiloscyllids), and fusion of the fourth and fifth epibranchials (also in galeomorphs). Only one ambiguous character, "bullae acoustica not distinct externally" (Holmgren, 1941, character 18) seems to unite the group. I am unable to come up with anything better, but provisionally retain the squaloids as a monophyletic group. The systematic position of *Pristiophorus* is left open. Characters used by Compagno (1977) are equivocal since they are not confined only to squaloids and pristiophoroids but the presence of small basal communicating canals (Holmgren, 1941, p. 69) would place *Pristiophorus* at or above node 3a.

I prefer not to formally diagnose new taxonomic units based on the characters I have used in view of the many questions that remain concerning their interrelationships. However, some informal names have been used and their relative ranking is indicated in figure 4.

COMMENTS ON THE RELATIONSHIPS OF BATOIDS

Living batoids have many distinctive differences from sharks, as is amply shown by Holmgren (1941) and more recently by Compagno (1973, 1977). These differences led Holmgren (1941, 1942) to propose a diphyletic origin of sharks and rays from placoderms, although corroborative evidence is slight (Moy-Thomas and Miles, 1971; Compagno, 1973). Holmgren's hypothesis is questionable in view of the large number of presumably derived characters shared by living batoids and sharks which do not occur in most fossil elasmobranchs (Schaeffer, in preparation, Maisey, in preparation).

Alternative proposals have been presented which attempt to ally batoids with certain living sharks, particularly *Pristiophorus* (Hoffman, 1913; Holmgren, 1941) and *Squatina* (Hasse, 1879–1885; Goodrich, 1909; Moy-Thomas, 1939). Since both genera are included in my group of orbitostylic sharks, some comments seem called for. Compagno (1973, 1977) has evaluated the evidence put forward in favor of Pristiophoroid and Squatinoid affinity of batoids, and shows much of it to be equivocal. Perhaps the most interesting similarities are found in the basibranchial skeletons of pristiophoroids and rhinobatoids (El Toubi and Hamdy, 1959; Compagno, 1973). However, batoids lack any of the orbitostylic features mentioned already and have their own distinctive jaw suspension (below). Batoids share certain negative characters, such as the absence of an anal fin, with *Squatina,* squaloids and *Pristiophorus*. I do not find the evidence for close affinity between batoids and orbi-

tostylic elasmobranchs to be very compelling. There is even less reason to suppose batoids and galeomorphs are sister groups. However, batoids and living sharks share many derived characters which suggest a close relationship, and are therefore regarded here as extant sister groups (essentially the conclusion reached by Compagno, 1973, 1977). The long enigmatic genus "*Protospinax*" has been placed in synonymy with *Belemnobatis,* a rhinobatoid (Maisey, 1976) and cannot therefore represent "a collateral ancestor of rays" (Compagno, 1973); the presence of finspines does not connect this form with basal squalomorphs, but represents a more primitive (phalacanthous) feature. It lacks the batoid synarcual and the centrum-free zone of *Spathobatis,* but retains an occipital half-centrum (one of many neoselachian synapomorphies). The palatoquadrates of *Belemnobatis annectans* lack an orbital process and consequently do not seem to have been orbitostylic.

VARIATION IN ELASMOBRANCH JAW SUSPENSION

A simple concept of hyostylic and amphistylic modes of jaw suspension is inadequate to encompass all the variation found in Recent and fossil elasmobranchs. Without introducing more confusing terminology, I will attempt a review of this variation.

1. Ethmoidal and postorbital articulation (no orbital process)

This occurred in many Paleozoic elasmobranchs, e.g., symmoriids, xenacanths (fig. 2C), *Goodrichthys,* and probably *Cladoselache.* The jaws are generally as long as or longer than the neurocranium, which may have a long (xenacanths) or short (symmoriids) otic region. The palatoquadrate has a deep otic process with a pronounced postorbital articulation. The palatine moiety of the palatoquadrate is sometimes very slender (symmoriids, *Cladoselache*). A small ethmoidal expansion (palatine process) of the dorsal surface apparently overlaps the suborbital shelf anteriorly in symmoriids and there is a trabecular articulation for such a process in xenacanths. A similar "orbital process" is noted in "*Xenacanthus*" and "*Cladodus*" (Jaekel, 1906; Gross, 1937; Jarvik, 1977), but it differs from the orbital process of living sharks in its relationship to other structures within the orbit, and should not be called an orbital process in the fossils. The dorsal margin of the otic process is directed laterally, but there is only a shallow concavity for the adductor mandibulae muscles. The palatoquadrates do not meet at the symphysis, and are apparently separated by the rostral cartilage.

The hyomandibula articulates proximally with the neurocranium, immediately anterior to the glossopharyngeal nerve, and meets the mandibular joint distally, thus giving some support to the jaws.

2. Ethmoidal and non-suspensory postorbital articulation (no orbital process)

Compagno (1977) reports this condition in the lamnoid *Pseudocarcharias kamoharai* (fig. 6A). The postorbital articulation disengages when the jaws are protracted. A short ethmoid groove accommodates the palatine part of the palatoquadrate. This condition may also have prevailed in *Synechodus* (fig. 6B). The postorbital articulation could not be very large (Woodward, 1886). *Palaeospinax* was undoubtedly similar, but doubt exists over whether an orbital process was present. There is a low eminence in *Synechodus* (Woodward, 1886), which may be an ethmoidal rather than orbital articulation. Although I interpreted *Palaeospinax* along these lines (Maisey, 1977), the "orbital process" of BM(NH) P3189 may simply be a crushed olfactory capsule or other cartilage fragment. Since there is no indication of a postorbital articulation in any specimen of *Palaeospinax,* it may have possessed reasonably protractile jaws.

3. Ethmoidal and hyomandibular support only

This pattern overlaps the previous one in that the palatoquadrate may (at least momentarily) contact the postorbital process in a number of traditionally "hyostylic" sharks (Compagno, 1977). The ethmoidal articula-

tion is relatively loose (fig. 6C) and easily disengages during jaw protraction, particularly in the more kinetic lamnoids and carcharhinids (Moss, 1962, 1972). Where protraction is more restricted and the palatoquadrates cannot make any postorbital contact, e.g., *Heterodontus* (fig. 6D) and orectoloboids, the ethmoidal articulation is much modified and strengthened while the ethmoid region retains a downturned embryonic posture into adulthood (Holmgren, 1941, 1942). There is a strong palatoquadrate symphysis or commissure.

4. Hybodontid hyostyly

Here, there is a strong ethmoidal articulation between palatoquadrate and ethmoid groove, rostral separation of the palatoquadrates so a symphysis does not develop, and the dorsal margin of the palatoquadrate is contoured to fit against the braincase from the ethmoid to the otic region. In *Hybodus basanus* (fig. 6E) there is no distinct postorbital articulation and the same may be true of many other *Hybodus, Acrodus,* and *Asteracanthus* spp.

Additional differences from neoselachians are found in the hyomandibula. This is enlarged and clearly had an important suspensorial function. However, its position relative to the palatoquadrate is unusual, since its ventral end meets the mandibular joints as in other sharks, but the shaft then passes dorsally over the palatoquadrate rather than mesial to it. Both an otic and an orbital process are absent, although an ethmoid process seems to be present in *Hybodus hauffianus* (Koken, 1907, fig. 1, pl. 2). In *Hybodus, Acrodus* and *Asteracanthus* a deep otic flange is developed, housing adductor mandibulae muscles, but there is little room for levator palatoquadrati muscles between palatoquadrate and braincase.

5. "Unsuspended" palatoquadrates

This extreme condition occurs only in batoids. The jaws are attached to the hyomandibula, but do not articulate directly with the neurocranium. In batoids (fig. 6F) the hyomandibula supports the outer edge of the jaws distally, and articulates with an extended depression on the auditory capsule proximally. The hyoid arch has no rays, and there is evidence that their blastemic tissue has instead given rise to a pseudo-hyoid arch between the hyoid and first branchial arch (Krivetski, 1917; DeBeer, 1932; Hamdy and Khalil, 1963). There is no ethmoidal, orbital, or otic process on the palatoquadrate although a quadrate groove is quite well developed in some batoids.

The batoid pseudohyal has the same presumably derived relationship to its efferent artery as the "pharyngobranchial" of chimaeroids (Patterson, 1965). However, these visceral arch structures have not been thoroughly reinvestigated.

6. Ethmoidal, orbital and postorbital articulation

This condition comes closest of all to amphistyly as Goodrich (1909) proposed, but it is confined to the hexanchoids (fig. 3C). A limited amount of mandibular kinesis is possible in *Hexanchus griseus* and *Notorhynchus maculatus* (Compagno, 1977; cf. Moss, 1972). The configuration of the orbital process has already been discussed.

In *Chlamydoselachus* the palatoquadrates are usually shown some distance from the postorbital process (Allis, 1923), but Compagno (1977) finds that there is a non-suspensory articulation which can disengage when the jaws are protracted forward and downward.

In fact, Allis's (1923) illustrations seem to be restorations rather than drawings of actual specimens. In Allis's plate VIII the hyomandibular articulation is correctly indicated but in plate VII the hyomandibula is drawn dorsal to its articulation, within the jugular groove (Schaeffer, personal commun.). A partially dissected head (AMNH, DVP teaching collection, K3-9) also reveals that the orbital process does not project into the orbit as much as Allis suggests, but lies with its medial surface in contact with a large facet anterior to the palatobasal process (figs. 3B, 5). When the jaws are protracted, the orbital process slides forward and downward between the articular facet and preorbital process. In this position the orbital process of the palatoquadrate is largely obscured by

the preorbital process of the braincase in lateral view (fig. 5B).

The hyomandibula of *Chlamydoselachus* is capable of sliding along its proximal articulation with the neurocranium (Garman, 1885; Smith, 1937). Although its distal extremity is bound to the mandible close to the jaw-joint (Allis, 1923; Smith, 1937), it was not regarded as a hyomandibula by Daniel (1934). Smith (1937) was undecided whether *Chlamydoselachus* was hyostylic or amphistylic, and Goodey (1910) regarded it as truly hyostylic. It would seem to be neither, or both, depending on whether its mouth is open or closed.

7. Ethmoidal and orbital articulation only

Squaloids, pristiophoroids, and *Squatina* all have an ethmoidal and orbital (palatobasal) articulation but lack a postorbital one. However, in *Aculeola* (a squaloid) palatoquadrates may contact the postorbital process temporarily during jaw protraction (fig. 6H).

A small upper Jurassic shark referred to *Protospinax* by Woodward (1919) was reinterpreted as a primitive galeomorph and named *Squalogaleus* (Maisey, 1976). At that time I adopted the traditional view that the absence of an otic process was a more important synapomorphy (of galeomorphs) than the presence of an orbital process which is widely but erroneously regarded as a primitive elasmobranch feature (fig. 6G). Instead, I now suggest *Squalogaleus* is an orbitostylic shark, and although its precise relationships are doubtful, its cranial outline is reminiscent of squaloids.

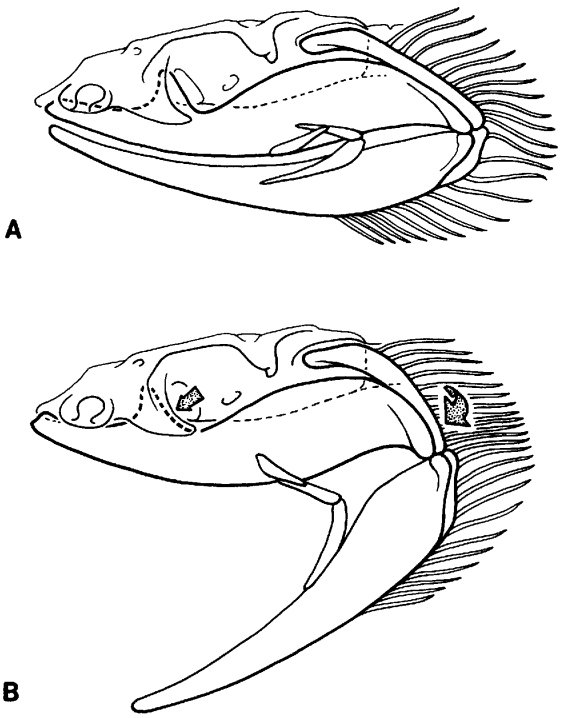

FIG. 5. *Chlamydoselachus* head, re-drawn from Allis (1923) to show the correct position of the hyomandibular articulation with the braincase, and of the orbital process on the palatoquadrate, also the direction and extent of jaw protraction (indicated by arrows in B).

SUMMARY

1. The hyomandibula primitively lends some support to the jaws in elasmobranchs, and to this extent is always functionally hyostylic.

2. Hyomandibular support for the jaws occurs in acanthodians, osteichthyans, and elasmobranch chondrichthyans. Therefore, there is a strong possibility that hyostyly is a primitive feature for all these gnathostomes.

3. Traditional views of jaw support emphasize some (but not all) variations in palatoquadrate attachment to the neurocranium, but ostensibly set out to illustrate differences in the amount of support given by the hyomandibula. As far as the hyomandibula is concerned, amphistylic suspension of Huxley (1876) and Goodrich (1909) is hyostylic. Examination of living sharks shows that there is no dividing line between "amphistyly" and "hyostyly" in the traditional sense.

4. The following features may be primitive to all gnathostomes as a corollary of jaws: a hyostylic hyomandibula attached to the mandibular joint, a spiracle rather than a complete hyoid gill-cleft, hyomandibula articulating with the otic region of the neurocranium, left and right palatoquadrates not meeting at a symphysis, ill-defined an-

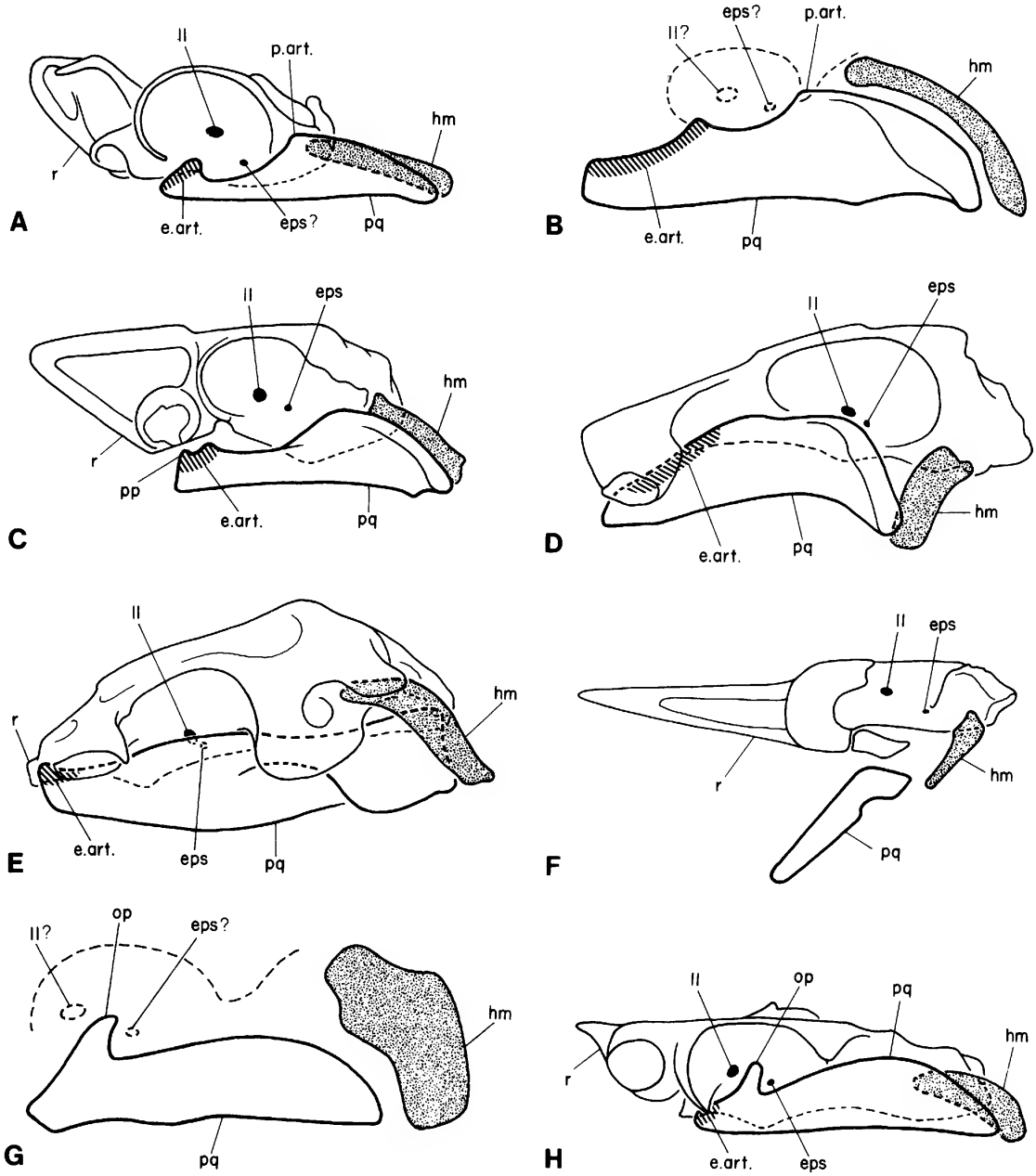

FIG. 6. Palatoquadrate and hyomandibular articulations in various fossil and Recent elasmobranchs referred to in the text. A, *Pseudocarcharias kamoharai* (after Compagno, 1977); B, *Synechodus dubrisiensis* (after Woodward, 1886); C, *Isurus* sp. (original); D, *Heterodontus francisci* (after Daniel, 1934); E, *Hybodus basanus* (original); F, *Raja* (after Hamdy and Khalil, 1963); G, *Squalogaleus woodwardi* (after Maisey, 1976); H, *Aculeola nigra* (squaloid), (original).

terior (ethmoidal, orbital) articulations between palatoquadrate and neurocranium, but well-developed postorbital articulation, and a double mandibular joint.

5. Several variations in jaw support can be distinguished among elasmobranchs on the basis of differences in attachments of the palatoquadrates to the neurocranium.

6. At least one of these patterns (orbitostylic suspension) seems to have systematic and phylogenetic importance. Squaloids, hexanchoids, *Chlamydoselachus, Squatina,* and *Pristiophorus* are considered to be members of a monophyletic group of orbitostylic neoselachians. Batoids have their own specialized suspension which is not orbitostylic.

7. Jaw suspension of orbitostylic neoselachians is not comparable with that of acanthodians or osteichthyans. This view is supported not only by embryological studies (Holmgren, 1942; Jollie, 1971a) but also by the topographical relationships of structures within the orbit. Jarvik's (1977) discussion of acanthodian relationships is consequently unconvincing.

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